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THE EFFICIENCY (WORK CAPACITY) OF NERVE COMPONENTS IN THE
CEREBRAL CORTEXES OF VARIOUS TYPES OF DOGS

Fiziologiya nervnykh
protsessov [Physiology
of Nerve Processes],
1955, Kiev, Pages 420-428

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In developing his theory on the types of higher nervous activity, I. P. Pavlov added to the list of fundamental properties of the elements of the cortex a new physiological characteristic of the state of a cortical cell: its efficiency.

In work on conditioned reflexes, special attention has to be given to this property of the cells of the central nervous system, as the level and duration of work capacity depends upon a correct balance of the processes of excitation and inhibition, the major physiological processes in the cerebral cortex. The balance between these processes determines the relationship between the reaction of nerve elements to the strength of a stimulus, i.e., their capacity to respond with a powerful reaction to powerful stimulus, with a weak to a weak, and also to respond repeatedly without loss of intensity to repetition of the identical stimulus.

In 1932 Pavlov wrote as follows on this property of nerve cells: "Cortical cells have a maximum capacity for work, beyond which point inhibition sets in to prevent excessive functional exhaustion. This maximum is not a constant, but a magnitude which changes in both acute and chronic fashion: in exhaustion, in hypnosis, in illness, and in old age."

Decline in the work capacity of cortical cells may arise as

the result of overstrain of the stimulatory or inhibitory processes by stimuli of excessive strength for the given nervous system, and as a result of disruption of the mobility of the major processes. Disruption of the mobility of the major processes may arise under various states of the organism: aging, nervous diseases resulting from overstrain of both basic processes and expressed in pathological states of individual portions of the cortex: in inertness of explosiveness of the stimulatory process. The appearance of inertness is the characteristic of an abnormally stable process of excitation even in the absence of reinforcement, while the state of outbursts is an increase in an effect which exists from the outset, but builds up rapidly, with sudden revulsion against food. I. P. Pavlov regarded this phenomenon as a state of lability in the process of excitation.

The development of the theory of types of higher nervous activity, and of the work capacity of cortical elements provided Pavlov with rich material for the study of various pathological states in animals and man. Pavlov was successful in artificially reproducing in dogs disorders of the higher nervous activity, and in clinical work he made observations of various pathological states in man. Discovery of the mechanism of pathological phenomena due to artificial destruction of the higher nervous activity in dogs, permitted an approach to the clarification of pathological states observed in man. This created the possibility of penetrating to the essence of pathological phenomena in man.

Our work has involved study of the reaction of components of the higher nervous system to various changes in customary load, as this load was increased and reduced in animals showing various types

of higher nervous activity. We confined ourselves entirely to the method of conditioned reflexes. An elaborated system of conditioned reflexes constituted the starting point and control for our observations. This system included a highly constant number of conditioned stimuli, the total time of the experiment as a whole, the time taken by isolated operation of the conditioned stimuli, and the interval between the individual applications of the conditioned stimuli (3 to 7 minutes). We use the term "state of efficiency" to designate the capacity of cortical elements to provide a corresponding reaction to a stimulus.

Our data permit the conclusion that the work capacity of cortical cells is a very labile property of the elements of the cortex, conditioned by the type of higher nervous activity, the functional state of the cerebral cortex, and the susceptibility of the cortical processes to adaptation. Our studies have provided data facilitating an understanding of the determination of work capacity in animals of various types. The changes observed in the higher nervous activity of dogs were analyzed by us in the light of Pavlov's teachings on the exhaustion of cortical elements, and the efficiency thereof. The repetition and fixing of a particular system of conditioned reflexes produces a given level of efficiency. Change in this system by elevated demands thereon interferes with the state of efficiency, and the elaboration of a new system meeting higher demands proceeds through adaptation to the fixing of new relationships. But the first days of elevated demands upon the basic processes may see a weakening of response reactions. G. V. Pol'bort believes the weakened effect of the supplementary stimulus to be based on the fact that the work capacity

of the cortical elements is inadequate for the newly-arrived supplementary stimulus to develop its effect to the full, with the result that work capacity is established on a higher level only gradually, as the demand for greater function is continued, i.e., via training. Thus, the cortical elements increase in efficiency with increase in the demands made upon them. This concept of G. V. Pol'bot has been further elaborated by A. M. Vorob'yev, A. A. Kramova, and O. M. Pugol'.

Our research has determined that the type of higher nervous activity is the governing factor in the elaboration of new systems with elevated demands upon the major nervous processes. With dogs of strong type, the cortical nerve elements show a high capacity for immediate adequate reaction to quantitative and qualitative changes in the system, without change in the strength of the response reaction. The cortical elements of weak dogs are subject to rapid exhaustion upon increase in tension thereon, as expressed in the reduction or complete absence of a response reaction. Under excessive loads, a pathological state may ensue. In studying the higher nervous activity, it is important to know the degree of efficiency of the cortical components. We have identified the degree of efficiency of cortical components by increasing and decreasing the load on the nerve components. We have experimented with increased load on the nerve elements:

- (1) by an increase in the quantity of stimuli applied;
- (2) by an increase in the duration of the intervals between the application of various conditioned reflexes; and
- (3) by an increase in the time of isolated action of the conditioned reflex.

After the experiment stereotype, consisting of a given quantity of stimuli, had been established, the number was increased to a doubling or trebling of the individual conditioned stimuli, or even to applying them 4 times in the course of an experiment, and finally doubling all the conditioned stimuli applied. Our methods of testing the load upon the working capacity of cortical components has demonstrated that animals with different types of nervous systems manifest entirely different reactions. Elevation in the demands made upon the cortical components of dogs of the strong type resulted in no disruption of the proper relationships in the magnitude of the conditioned reflexes. Their work capacity is great, and an additional stimulus calls forth a high response reaction.

We observed an entirely different phenomenon when placing increased pressure upon the work capacity of the cortical elements of dogs of the weak type. Doubled or trebled application of the conditioned stimuli in the course of an experiment invariably produced disturbance in conditioned-reflex activity. The required relationships between response reactions and the strenght of the conditioned stimuli disappeared. The conditioned reflexes revealed change not only on the day when experiments under increased load were run, but for a long period in subsequent experiments, without supplementary stimuli. We observed in representatives of the weak types that elevation of the demands upon work capacity at one point was reflected at neighboring points, resulting in reduction of the conditioned reflexes on repetition, and even in their disappearance. We regarded these changes in conditioned reflexes as manifestations of defensive inhibition, while reduction in the conditioned reflexes at neighboring points was regarded as irradiating inhibition (see Table).

The state of efficiency of cortical components to a given system of stimuli is conditioned by a number of factors. They include the quantity of stimuli applied, and all the manipulations involved in the running of the experiment (the chamber, straps, stand, etc). Study of the efficiency of cortical elements by means of an increase in the length of the intervals between individual stimuli, and an increase in the period of isolated action by the conditioned reflex shows the duration of the effect of the stimulus, and that of the interval between individual actions also to be effected by efficiency. Changes in the duration of the experiment by increasing the intervals between all the conditioned reflexes applied, or by increasing one of the intervals to 10 minutes instead of the normal 3 to 5, always resulted in inhibition. And when the experiment takes this form, we observed differences in the reactions of animals with different types of nervous activity.

In animals of the strong type, this load on their work capacity does not result in exhaustion of the cortical elements and development of profound inhibition. But in weak animals this load on work capacity resulted in exhaustion of the work capacity of the cortical elements and the onset of profound inhibition. Variation of the experiments in different directions provided us with new data for a Pavlovian understanding of this question.

Tests of strain on work capacity may be run not only by raising, but also by weakening, the load applied to nerve components. This is done by omitting various stimuli or by applying only a portion of the complex employed in the normal experiment.

Analysis of the data provides reason to believe that the

very tiniest details of the experimental environment affect the state of efficiency of cortical elements. Here we take as our starting point I. P. Pavlov's concept of the organism as a unitary structure. "In the final analysis," he wrote, "both an atom and an organism are merely relatively individualized portions of the environment." Pavlov analyzed all the phenomena of nature from the viewpoint of determinism. He noted that all external influences leave their mark on the higher cortical elements.

In a series of experiments we have studied the effect of the total environment accompanying the experiment, and the effect of a greater amount of ordinary rest upon conditioned-reflex activity. The experiment was run as follows. After the formation of a system of conditioned reflexes and long-term observation of the state of the level of its conditioned reflexes, a dog was brought into the chamber, the straps and collar were attached, the bulb was put in place by adhesive, i.e., all the manipulations were performed which normally preceded the start of an experiment. Then the dog was fed, without applying the conditioned reflex, whereupon it was led out of the chamber. The next day, when the experiment was run in its usual form with use of all the conditioned reflexes, we witnessed an increase in the conditioned reflexes over the usual standard. This increase in reflexes might well result as a result of the rest given to the cortical elements. In order to study these phenomena we investigated the effect of rest upon these animals. Over a period of many months we sustained the system of conditioned reflex for 6 consecutive working days, and permitted the animal to rest on the seventh. By means of an elaborated, regularly reinforced system, we permitted the dog additional rest in the middle of the week, and omitted an experiment. Omitting an experiment in the middle of the

weak also resulted in increased conditioned reflexes, but it was specifically when the experiment was conducted in this manner that the degree of strain upon the work capacity of dogs of various types made itself felt.

In dogs of the weak type, supplementary rest during the week exerted a greater effect than when the work capacity of the cortical components was tested by applying only a portion of the complex, i.e., bringing the dog into the room, performing all manipulations, but not conducting the experiment.

Our understanding of these phenomena is based on the Pavlovian concept of the exhaustibility of cortical cells. The cortical cells of animals of the weak type are weak, and operate to the limit of their capacity when subject to conditioned stimuli for long periods of time. Therefore, complete rest is highly effective, due to the removal of the component of defensive inhibition.

In strong-type dogs the cortical cells are of low exhaustibility, and supplementary rest -- omission of one day of experiments, with the system of conditioned reflexes usually applied -- does not result in an increase in conditioned reflexes on the next day. This is explained by the absence, in the usual experiments, of transmarginal inhibition, so that supplementary rest does not produce any significant elevation of reflexes in strong-type dogs. However, on the day after experiments in which only a portion of the complex was applied, the conditioned reflexes of these dogs functioned on a considerably higher plane than on the preceding days.

This makes quite clear the significance of the state of

efficiency for each particular level of the factors accompanying the experiment. The arrangement of the room in which it is conducted, the preliminary manipulations, the specific system of conditioned reflexes all combine to form in the large hemispheres of the animal a single complex stimulus, or stereotype, setting up a specific level of excitability in the cortex and determining the work capacity of the components thereof.

**TESTS OF THE EFFICIENCY OF CORTICAL ELEMENTS BY INCREASE
IN STIMULI**

<u>Dog</u>	<u>Conditions of Experiment</u>	<u>Stimuli</u>	
Ryabchik	Usual magnitude of conditioned reflex	loud tone	light
		32	39
	Magnitude on repetition of stimulus	expt 216	expt 225
		32	25
Bystryi		35	27
	Usual magnitude of conditioned reflex	bell	metronome
		25	38
	Magnitude on repetition of stimulus	expt 109	expt 150
Dzhil'ka		25	38
		24	37
	Usual magnitude of conditioned reflex	life	gurgling
		22	20
Kashta.	Magnitude on repetition of stimulus	expt 188	expt 200
		24	20
		02	04
	Usual magnitude of conditioned reflex	life	light
Kashta.		25	12
	Magnitude on repetition of stimulus	expt 163	expt 175
		26	11
		02	00
Dzhul'ka	Usual magnitude of conditioned reflex	gurgling	
		20	
	Magnitude on repetition of stimulus	expt 87	
		gurgling	
		20	
		09	

The animal's behavior is always the result of complex activity in the central nervous system. The fact that behavior

constitutes a response to all factors in combination is facilitated by the action of the cortex in synthesis, this being conditioned by the respective influences of interoceptive and exteroceptive stimuli.

"It is quite clear to us," wrote I. P. Pavlov, "that the cerebral cortex is a complex functional mosaic of individual components, each of which exercises a specific positive or inhibitory physiological effect. On the other hand, it is also clear that all the components are combined at each given moment into a system in which each element acts in interrelation with all the others."

The external environment, combined with the constantly changing internal environment, conditions the intensity and the order of conditioned reflexes, and also the changes in cortical states observed in the experiments.

These fundamental Pavlovian propositions emerge clearly in our experiments, providing new data as to the significance of the activity of the large hemispheres in synthesis. By studying the effect of omission of individual stimuli, we see that an increase in excitability occurs only if particular points constituting part of a unified complex stimulus in the experiment be affected. If the animal was given supplementary rest during the week, its conditioned reflexes the following day would be stronger only in response to those stimuli which require ultimate strain. Here, rest facilitates restoration of function in cortical elements. This pertains to experiments with animals with the weak type of nervous system. In strong-type animals, under conditions in which the cortical components of the central nervous system are not strained to the utmost, supplementary rest does not produce noticeable changes in overall conditioned reflex activity.

When the animal was brought into the room, and placed in the stand, but the experiment was not run, the following day revealed a marked increase in all conditioned reflexes. This is a result of the fact that the general stereotype had been affected, and a stimulus had gone into operation which set in motion the entire chain of phenomena operative in the presence of the conditioned reflex stereotype.

Conclusion

Our research provides data contributing to an understanding of the state of efficiency in animals of various types. A well-elaborated stereotype facilitates normal higher nervous activity, and the very slightest changes therein produce changes in the usual higher nervous activity in all types of animals.

In studying the higher nervous activity by the method of conditioned reflexes it is necessary to take into account not only the type of higher nervous activity, and whether the cerebral cortex is in a normal or pathological state, but also the level of efficiency and training of the cortical components to the given state stereotype. The data we have obtained presents a clear picture of the fact that, in long-term functioning, animals of various types of higher nervous activity are capable of developing a level of efficiency which depends upon the strength of the various nervous processes. The level of efficiency at the beginning of training is completely dependent upon the type of higher nervous activity. Continued training of the cortical processes and long-term reinforcement of the stereotype enable animals having a weak type of nervous system also to present regularly a proper picture of response reactions, with the result that the central nervous

system of these animals has reserve capabilities of adaptation to the demands of the environment. In animals of the weak type the higher nervous activity is capable of standardization within the limits of the given work capacity. Change in the normal environment or disturbance of any component of the stereotype produces a higher nervous reaction in animals, regardless of type. Typological differences emerge most clearly under such conditions. When disturbance in stereotype is minor, typological peculiarities are revealed primarily in quantitative relationships. When changes in stereotype are more profound and demands upon the basic processes are elevated beyond the bounds of work capacity, the differences take on a qualitative nature. In animals of strong type, various changes in stereotype, not acute in nature, produce changes in conditioned reflexes which pass rapidly. In weak-type animals, similar changes in stereotype produce more profound, and, sometimes, pathological changes in conditioned reflex activity.

Tests of the work capacity of cortical elements by means of changes in stereotype demonstrate that in animals having the strong type of nervous system, the cortical elements have greater work capacity, and respond to influences designed to increase them, by an increase in efficiency. In animals of the weak type, the cortical components are of low work capacity and high exhaustibility. Therefore the posing of elevated demands thereon produces rapid exhaustion, followed by inhibition, and even a breakdown of higher nervous activity. In determination of the work capacity of cortical elements of the weak type, significance adheres to the time during which the system is reinforced, and the preceding level of intensity of the work capacity of the nervous elements. When all stimuli are applied twice, the presentation of

elevated demands on the work capacity of the cortical elements results in more severe breakdowns in conditioned-reflex activity than when conditioned stimuli are applied but once.

Dogs of both types present the possibility of increasing work capacity. In animals of strong types the elaboration of a new state of efficiency of the cortical components occurs rapidly and reveals no phasic phenomena. In weak types of animals the elaboration of a new state, requiring greater stress on the cortical components, proceeds by phases.